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THE BEGGING BEHAVIOR OF NESTLING EASTERN SCREECH-OWLS

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ABSTRACT.—The behavior of adults and nestlings at nine Eastern Screech-owl (*Otus asio*) nests in central Kentucky was monitored by videotaping the owls in specially-constructed nest boxes. Adult screech-owls delivered 1281 prey items during 164 h of taping. Nestlings fed first by adults started to beg significantly earlier, extended their beaks higher and closer to the adult, and called at higher rates and with greater volume than did siblings that were not fed first. In addition, nestlings fed first started begging earlier, stretched their beaks higher, positioned their beaks closer to the adult, and vocalized at a higher rate than when they were not fed first. In addition, after being returned to the nest, nestling screech-owls temporarily deprived of food begged with greater intensity and were fed more often than siblings. Such results provide further evidence for the positive relationship between hunger, begging intensity, and the chances of being fed. Our results also indicate, however, that nestling mass may be important in determining which nestlings will be fed when differences in the mass of siblings reach a certain level. We observed no siblicide or other aggression between siblings. Contributing to this absence of aggression may have been the large boxes used for videotaping and an abundant food supply. It is also possible, however, that aggression and siblicide occur infrequently in broods of screech-owls. *Received 28 Dec. 1996, accepted 29 July 1997.*

Evidence is accumulating that parental provisioning behavior can be influenced by nestling behavior (Stamps et al. 1985, 1989; Wright and Cuthill 1989; Teather 1992). Altricial nestlings may improve their chances of being fed by seeking a particular position in the nest, reaching higher and closer to the visiting adult, and vocalizing first or with the greatest intensity (e.g., Smith and Montgomerie 1991, Teather 1992). Such behavior may be correlated with hunger level. For example, Smith and Montgomerie (1991) experimentally prevented parents from feeding nestling American Robins (*Turdus migratorius*) and found that both the intensity of begging and the number of feedings subsequently received by food-deprived nestlings increased.

Begging intensity may not be the only factor that determines which nestling will be fed by adults; size may also play a role. For example, small Yellow-headed Blackbird (*Xanthocephalus xanthocepthalus*) nestlings beg more than larger siblings but are fed less (Price and Ydenberg 1995). Similar results have been reported in other species where siblings differ in size as a result of asynchronous hatching (e.g., Ryden and Bengtsson 1980).

Among raptors and other species where nestlings possess "weapons" (beak and talons), access to food delivered by parents also can be influenced by direct interactions among siblings. For example, Allen (1924:4–5) observed three nestling Eastern Screech-Owls (*Otus asio*) competing for access to a prey item (a bird) and reported that "after one such tug-of-war . . . two of the young attacked the third and picked most of his bones by morning."

With the exception of Allen's (1924) limited observations, little is known about the behavior of nestling Eastern Screech-Owls and, specifically, how nestlings gain access to the food delivered by parents. The objective of our study was to examine the begging behavior of nestling screech-owls and, more precisely, to determine the importance of begging behavior and nestling size in the distribution of food to nestlings by adult screech-owls.

Eastern Screech-Owls are socially and genetically monogamous (Lawless et al. 1997). Both adults feed nestlings and the most common prey delivered to nestling screech-owls in central Kentucky include beetles, crickets, and beetle larvae (Hofstetter 1995). Adults typically feed nestlings at the cavity (or nestbox) entrance and one nestling is usually fed per visit (Hofstetter 1995). The nestling period averages about 28 days (Gehlbach 1994, pers. obs.).

STUDY AREA AND METHODS

We conducted this study at the Central Kentucky Wildlife Management Area, located 17 km southeast of Richmond, Madison County, Kentucky. During March and April 1994, we checked nest boxes and

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natural cavities for incubating or brooding female screech-owls. Once located, nests (n = 9) were monitored until nestlings were 11–14 days old. Nestlings and the adult female at each nest were then transferred into nest boxes designed for video-taping. These video-taping boxes were placed in the same location as, or immediately adjacent to, the nest cavity or nest box.

Video-taping boxes had a chamber (20 × 31 × 41 cm) for the owls and a larger one for a camcorder. The smaller chamber was equipped with two small fluorescent lights to permit taping at night. The camcorder was set at a 25–30° downward angle from the horizontal to permit video-taping of both the nestlings and the visiting adult.

At the time of transfer, each owlet was banded with a U.S. Fish and Wildlife Service numbered aluminum leg band and uniquely color-marked on the top of the head using colored "Sharpie" markers. We also collected 200–400 µl of blood from each nestling for use in another study (Lawless et al. 1997).

Video-taping generally began the day after owls were transferred to the video-taping boxes and continued until the young owls fledged. Video-taping sessions were 2–4 h in duration, with each tape lasting 2 h. All taping occurred during the period from just prior to sunset (about 20:30) until 01:30.

All video-tapes were subsequently viewed and analyzed using a Sony video recorder/player (Model SLV-701HF) and a 19 inch color television. During analysis of the tapes, we quantified the begging behavior of nestlings and determined how parents allocated food among nestlings. The begging intensity of individual nestlings was ranked in a manner similar to that described by Smith and Montgomerie (1991). For each visit by a parent to the nest, each nestling was ranked based on several behaviors, including: (1) when the nestling started to vocalize after the parent's arrival (start rank), (2) the height to which each nestling extended its bill (height rank), (3) the distance of the nestling's bill from the parent (position rank), (4) the vocalizing rate (rate rank), and (5) the volume (or intensity) of vocalizations (volume rank). Height and distance ranks were estimated at the instant a parent arrived at the nest box entrance. The vocalizing rate was determined by counting the number of calls (with a call defined as any continuous sound) during the period between the parent's arrival and the feeding of a nestling. The relative volume of each nestling's calls during the period between a parent's arrival and the feeding of a nestling was estimated and ranked. For each parental visit, therefore, each nestling's relative begging intensity was determined using its rank scores.

Because brood size varied from 2–5, ranks were not comparable between nests. Therefore, as suggested by Smith and Montgomerie (1991), ranks of begging intensity were standardized to [(rank − 1)/(brood size − 1)], where 1 is the lowest and 5 the highest rank. Standardized ranks, therefore, varied from 0 to 1, with a lower standardized rank indicating more intense begging.

Nestlings were weighed every other day. To examine the possible effects of nestling mass on the behavior of nestlings and adults, nestlings were categorized as "small," "medium" and "large" in broods where the difference between the mean mass of the lightest and heaviest nestlings was at least 9 g (n = 19 nestlings from six broods). The mean difference in mass of large and small nestlings at these six nests was 21.5 g (range = 9.2–51 g). Small nestlings (n = 8) had a mean mass of 99.7 ± 3.4 g, medium nestlings (n = 3) 107.8 ± 3.3 g, and large nestlings (n = 8) 115.5 ± 2.8 g. These differences in mass were significant ($F_{2,21}$ = 15.3, $P < 0.001$).

To determine the effect of nestling hunger level on the begging behavior of nestlings, randomly-selected nestlings (one from each of four nests) were temporarily removed from their nest boxes and, thus, were not fed for 2 h. These nestlings were returned to their nest box, positioned randomly with respect to the entrance and their siblings, and the nest was then videotaped for at least two additional hours. These tapes were then analyzed in the manner described previously.

Wilcoxon rank sum tests (SAS Institute 1989) were used to compare the ranks of (1) nestlings fed first versus siblings not fed, and (2) nestlings fed first versus the ranks of the same nestlings when not fed. Ranks of small, medium, and large nestlings were compared using repeated measures analysis of variance (SAS Institute 1989). Likelihood ratio χ^2 tests were used to determine if nestlings (either experimental versus non-experimental nestlings or small, medium, and large nestlings) were fed in a non-random manner. Statistical analyses were performed using the Statistical Analysis System (SAS Institute 1989). All values are presented as mean ± one standard error.

RESULTS

Nine screech-owl nests were videotaped on 33 nights for a total of 164 h. Each nest was taped for an average of 18.2 ± 4.2 h (range = 8–32 h). Adult screech-owls delivered 1281 prey items, with an average of 142.3 ± 52.5 prey items delivered per nest (range = 36–404 prey items). Adults always delivered one prey item per visit and typically fed just one nestling per visit (98.1% of all visits). Adult screech-owls (male and female combined) delivered prey to nestlings an average of 8.80 ± 0.97 times per hour.

Nestling begging behavior.—To determine if the begging intensity of the first nestling to receive food during a parental visit differed from that of its siblings, we compared the ranks of the nestling fed first with the average rank of its siblings. Using one randomly-chosen nestling from each nest, we also compared the mean ranks of nestlings when fed first to the ranks of that same nestling when not fed

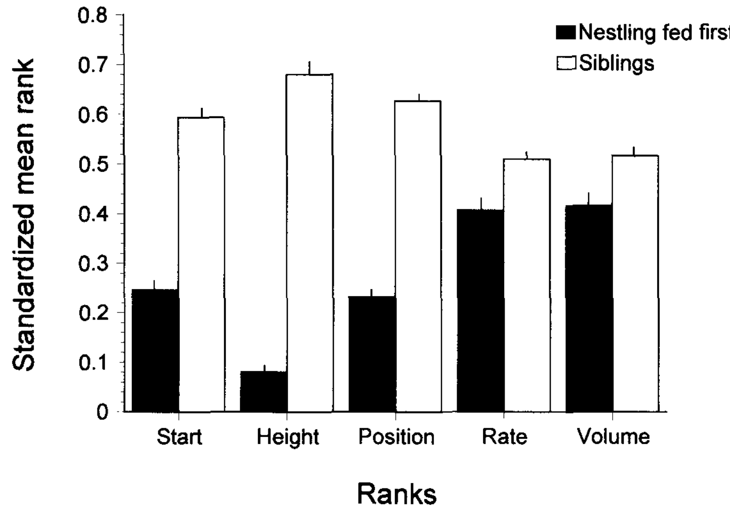

FIG. 1. Standardized mean ranks of nestling screech-owls fed first and those of siblings not fed first. See text for definition of terms.

first. Nestlings that were fed first started to beg significantly earlier ($z = 25.1$, $P = 0.001$), extended their beak significantly higher ($z = 41.4$, $P = 0.001$), and held their beaks significantly closer to the adult ($z = 28.4$, $P = 0.001$) than siblings that were not fed (Fig. 1). Nestlings fed first also gave significantly louder calls ($z = 6.5$, $P = 0.001$) at a significantly greater rate ($z = 6.6$, $P = 0.001$) than nestlings that were not fed (Fig. 1).

The rankings for randomly chosen nestlings (one from each of the nine nests) when fed first were also compared to their rankings when not fed (Fig. 2). Nestlings fed first started begging significantly earlier ($z = 13.3$, $P = 0.001$), stretched their beaks significantly higher ($z = 25.2$, $P = 0.001$), positioned their beaks significantly closer to the adult ($z = 15.1$, $P = 0.001$), and vocalized at a significantly higher rate ($z = 3.0$, $P = 0.0031$) than

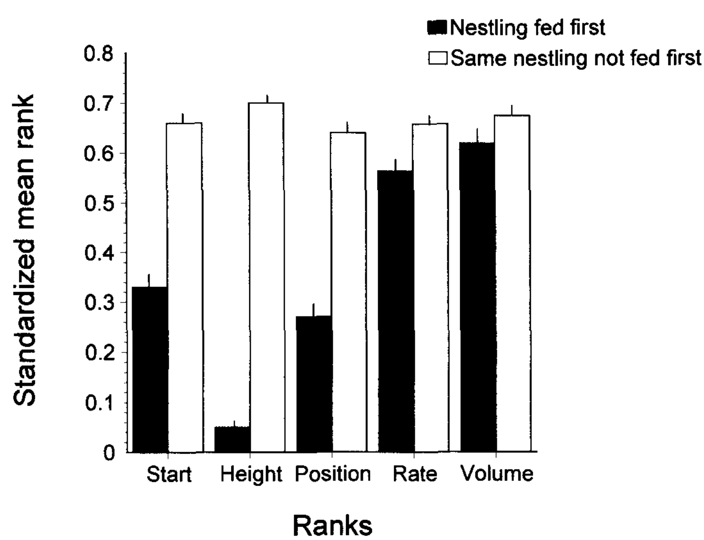

FIG. 2. Standardized mean ranks of individual nestling screech-owls when fed first and of the same nestling when not fed first.

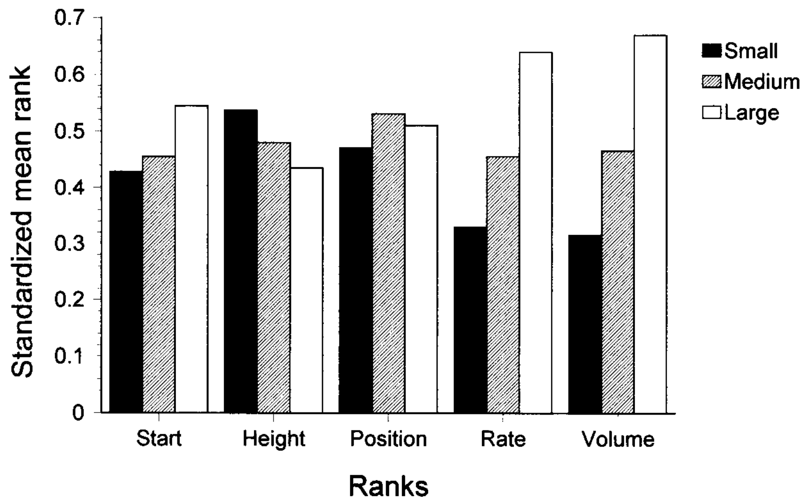

FIG. 3. Standardized mean ranks of small, medium, and large nestling screech-owls.

when not fed. However, nestlings fed first did not call with greater volume (z = 1.5, $P > 0.05$) than when not fed.

Nestling mass.—For all six nests in which young were categorized by mass, the standardized mean ranks of small, medium, and large nestlings did not differ significantly (repeated measures ANOVA, $P > 0.05$; Fig. 3). Analysis of individual nests revealed significant differences in mean standardized ranks of siblings at only one nest (Nest 8; Wilcoxon tests, $P < 0.001$). Two nestlings were present at this nest and these nestlings differed substantially in mean mass (108 g versus 57 g). Comparison of these two nestlings indicates that, upon arrival of an adult with food, the smaller one generally started begging earlier, was positioned closer, and called with greater volume and at a greater rate (Fig. 4). However, the larger nestling almost always extended its beak higher (Fig. 4).

Overall, the distribution of feedings among small, medium, and large nestlings was significantly non-random (χ^2 = 22.7, df = 2, $P < 0.001$; N = 6 nests), with adults feeding large nestlings more frequently than expected

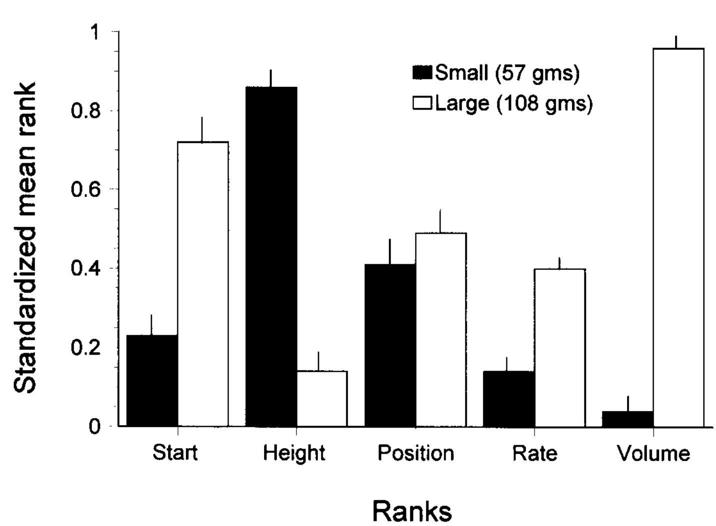

FIG. 4. Standardized mean ranks for the small and large nestlings at Nest 8.

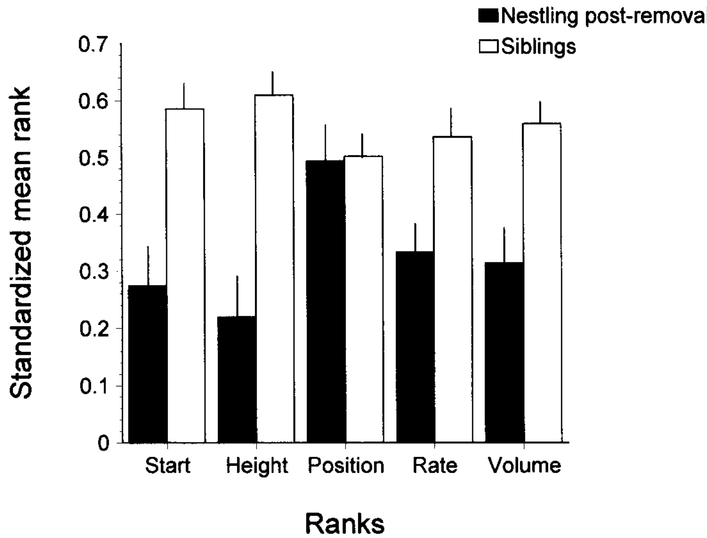

FIG. 5. Standardized mean ranks of temporarily-removed nestling screech-owls (food deprived) and those of siblings that were not removed (not food deprived).

and small nestlings less frequently than expected. Examination of individual broods revealed, however, that differences in the distribution of feedings among nestlings was significantly non-random only at Nest 8. Of 145 prey items delivered by adults, the large nestling obtained 117 (80.7%) (χ^2 = 117.4, df = 1, $P < 0.001$).

For the remaining five nests, small, medium, and large nestlings were fed a similar number of times (χ^2 = 0.7, df = 2, $P > 0.05$). The difference in mean mass of the smallest and largest nestlings at these five nests was 9.2, 12, 14, 15.5, and 27.5 g, respectively.

Nestling removal.—Nestlings prevented from eating for a 2 h period begged with significantly greater intensity than their siblings after being returned to the nest (Fig. 5). Four of five begging indices were significantly lower for such food-deprived nestlings than for their siblings (start rank, height rank, volume rank, and rate rank; Wilcoxon tests, $P <$ 0.027). The position rank of food-deprived nestlings did not vary from that of siblings (z = 0.1, $P > 0.05$).

Food-deprived nestlings (N = 4) were fed more often (χ^2 = 13.6, df = 1, $P < 0.001$) than siblings (N = 10) during the 2 h period after being returned to the nest. Food-deprived siblings (N = 4) received 55.2% of all prey delivered to their nests during that period.

Nestling aggression and mortality.—Previous investigators have reported facultative siblicide by nestling Eastern Screech-Owls (Allen 1924, Gehlbach 1994). During 164 h of observation, however, we saw no direct aggression (grabbing with talons or biting) among siblings either during or between feedings.

One nestling apparently died shortly after being transferred to a video-taping box. This nestling, noticeably smaller than its two siblings, disappeared within 24 h after transfer so we had not yet started videotaping. At the time of transfer we noticed no injuries or wounds. It is likely that this nestling died of starvation and, because no remains were found, its carcass was probably cannibalized.

DISCUSSION

Adult screech-owls were more likely to feed a nestling that started begging earlier, extended its beak higher and closer to the visiting adult, and called at a greater rate and with greater volume than did its siblings. In addition, after being returned to the nest, nestling screech-owls deprived of food begged with greater intensity and were fed more frequently than siblings (who were fed by parents in the absence of their sibling). Such results agree with the findings of other investigators (Smith and Montgomerie 1991, Redondo and Castro 1992, Price and Ydenberg 1995) and provide further evidence for the positive relationship between hunger, begging intensity, and the chances of being fed.

Our results also indicate that nestling size or mass may be important in determining which nestling will be fed by adults. At one nest with two young (Nest 8), the smaller nestling consistently begged with greater intensity than the larger nestling but the larger nestling still obtained 80.7% of the prey delivered by adults. Observations of this nest in conjunction with those at the other nests reveal two features of screech-owl begging behavior. First, the ability of a nestling to extend its bill higher than siblings appears to be the most important factor in determining which nestling screech-owl will obtain food from an adult. At Nest 8, the smaller nestling consistently started begging earlier, positioned itself closer to the adult, and uttered louder vocalizations at a higher rate than its larger sibling. Despite such behavior, the larger nestling reached higher and received most of the food. Given that screech-owls typically nest in natural cavities and that adults entering a cavity with food would typically approach nestlings from above, reaching higher than siblings would appear to be the best strategy for a nestling screech-owl seeking to obtain food. Second, differences in the size or mass of siblings apparently must be above some minimum value before influencing the distribution of food. At five nests where differences in the mass of smallest and largest nestlings ranged from 9.2–27.5 g (or where the mass of the smallest nestling ranged from 78.4–92.1% of the mass of the largest nestling), nestling mass had no apparent effect on the chances of a nestling obtaining food. Only at the nest where the difference was 51 g (and the mass of the smallest nestling was 52.8% of the mass of the larger nestling) did nestling mass influence the distribution of food. Thus, our results indicate that size may begin to influence the distribution of food to nestling Eastern Screech-Owls when the mass of the smallest nestling is somewhere between 52.8 and 78.4% that of its largest sibling.

Our results indicate that small nestling screech-owls may beg more vigorously than larger siblings (particularly vocally) yet receive less food. Similar observations have been reported in other species that exhibit asynchronous hatching and, therefore, size asymmetries among nestlings (Bengtsson and Ryden 1981, Drummond et al. 1986, Price and Ydenberg 1995). Although calling rate and volume appear to be less important than other behaviors (e.g., beak height) in determining which nestling screech-owl receives food, nestling vocal behavior may influence parental foraging behavior. For example, Bengtsson and Ryden (1983) found that adult Great Tits (*Parus major*) increased feeding rates during periods when recorded calls were played during feeding visits to the nest. Thus, the higher calling rates of small nestling screech-owls may improve their chances of getting some food by increasing the number of feeding visits by adults.

We observed no overt aggression between siblings. In contrast, Allen (1924) observed one case of siblicide. In addition, although no direct observations were made, Gehlbach (1994:116) reported that small nestlings sometimes disappeared from nests during their first 15 days post-hatching and suggested that they "suffered probable fratricide (siblicide) or infanticide and invariable cannibalism . . ." Gehlbach (1994) further suggested that some nestling screech-owls die from starvation and suffocation. One possible reason why we observed no aggression is that our videotaping boxes were relatively large and, as a result, nestlings were not "crowded." Gehlbach (1994) found that greater "brood crowdedness" (more nestlings relative to the size of a cavity or nest box) increased the likelihood of nestling mortality (and, perhaps, the likelihood of siblicide). Another possible reason why we observed no aggression between siblings is that adults provided nestlings with sufficient food. Previous studies suggest that additional food may diminish nestling mortality in facultatively siblicidal species (Mock et al. 1987, Magrath 1989). Finally, it is possible that siblicidal behavior is simply uncommon in Eastern Screech-Owls and that starvation and suffocation are the primary causes of mortality among nestlings.

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